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Thermal trait variation may buffer Southern Ocean phytoplankton from anthropogenic warming

Ian W. Bishop[1] | **Stephanie I. Anderson**[1] | **Sinead Collins**[2] | **Tatiana A. Rynearson**[1]

[1]Graduate School of Oceanography, University of Rhode Island, Narragansett, Rhode Island, USA

[2]Institute of Evolutionary Biology, University of Edinburgh, Edinburgh, UK

Correspondence
Tatiana A. Rynearson, Graduate School of Oceanography, University of Rhode Island, Narragansett, RI 02882, USA.
Email: rynearson@uri.edu

Present address
Stephanie I. Anderson, Department of Earth, Atmospheric, and Planetary Sciences, Massachusetts Institute of Technology, Cambridge, Massachusetts, USA

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Abstract

Despite the potential of standing genetic variation to rescue communities and shape future adaptation to climate change, high levels of uncertainty are associated with intraspecific trait variation in marine phytoplankton. Recent model intercomparisons have pointed to an urgent need to reduce uncertainty in the projected responses of marine ecosystems to climate change, including Southern Ocean (SO) surface waters, which are among the most rapidly warming habitats on Earth. Because SO phytoplankton growth responses to warming sea surface temperature (SST) are poorly constrained, we developed a high-throughput growth assay to simultaneously examine inter- and intra-specific thermal trait variation in a group of 43 taxonomically diverse and biogeochemically important SO phytoplankton called diatoms. We found significant differential growth performance among species across thermal traits, including optimum and maximum tolerated growth temperatures. Within species, coefficients of variation ranged from 3% to 48% among strains for those same key thermal traits. Using SO SST projections for 2100, we predicted biogeographic ranges that differed by up to 97% between the least and most tolerant strains for each species, illustrating the role that strain-specific differences in temperature response can play in shaping predictions of future phytoplankton biogeography. Our findings revealed the presence and scale of thermal trait variation in SO phytoplankton and suggest these communities may already harbour the thermal trait diversity required to withstand projected 21st-century SST change in the SO even under severe climate forcing scenarios.

KEYWORDS
adaptive potential, diatoms, intraspecific diversity, phytoplankton, Southern Ocean, thermal performance traits

1 | INTRODUCTION

The surface waters of the Southern Ocean (SO) have experienced rapid warming over the past 50 years (Gille, 2008; Meredith & King, 2005) and are predicted to increase in temperature by 1–4°C by 2100 (Moore et al., 2018; Tittensor et al., 2021). The warming SO is home to taxonomically diverse phytoplankton communities (Constable et al., 2014) that support a highly productive and efficient marine polar food web (Clarke, 1985; Clarke et al., 2007). Changes in phytoplankton species composition, distribution, and productivity, in response to shifting sea surface temperatures (SSTs), may directly affect key processes that this community modulates, including processes as diverse as macronutrient resupply to surface waters in temperate and tropical regions of the world's oceans (Sarmiento et al., 2004), deep sea carbon export (Assmy et al., 2013), and the distributions and production of keystone marine macroinvertebrates (Rogers et al., 2020).

In general, phytoplankton may respond to a changing thermal seascape in one of three ways: "move, adapt or die" (Maggini et al., 2011). These options are further limited for cold-adapted polar phytoplankton because "moving" (i.e., tracking the temperatures to which they are already adapted) is likely untenable, as they already inhabit the coldest sunlit regions of the ocean. It is therefore suggested that adaptation will play a prominent role in the persistence of cold-adapted phytoplankton in response to sea surface warming (Reusch & Boyd, 2013). Such adaptation draws on two primary sources of genetic variation: de novo mutation and standing genetic diversity (Bell, 2008). Both sources of genetic variation can shift average phenotypic traits such as the optimum and maximum growth temperatures to match environmental conditions (e.g., Lohbeck et al., 2012; Padfield et al., 2016). De novo mutation yields novel genetic variation over time, and is dependent on a combination of mutation rates, generation times, and population sizes, whereas standing genetic variation represents variation already present in a population and is not dependent on the generation of new mutations (Barrett & Schluter, 2008). In general, de novo mutation increases in adaptive importance over longer time frames, while standing genetic variation can be acted on by natural selection immediately (Bell, 2008), though heritable epigenetic effects and transgenerational plasticity may also provide rapidly-available variation on which natural selection can act (Danchin et al., 2019). Phytoplankton have short generation times (hours to days) and large population sizes (Krasovec et al., 2019; Mock et al., 2017), which allow for efficient lineage sorting of standing genetic variation that can have measurable impacts on population growth rates (Scheinin et al., 2015).

Despite the potential of standing genetic variation to rescue communities and shape future adaptation (Des Roches et al., 2018; Violle et al., 2012) and its increasingly recognised role in climate-related eco-evolutionary dynamics of phytoplankton (Collins et al., 2014; Rynearson et al., 2022), the intraspecific trait variation that standing genetic variation produces is still poorly constrained in marine phytoplankton (Boyd et al., 2013; Godhe & Rynearson, 2017). This is particularly true for standing variation in thermal traits. Generally, researchers have focused on characterising inter- rather than intraspecific thermal trait variation, with only a handful of species physiologically characterised beyond the testing of a single representative strain (Anderson et al., 2021; Thomas et al., 2012). Relatively few studies have reported thermal functional traits for SO phytoplankton (Figure 1; Table S1) and none of them assayed multiple strains to determine within-species thermal trait variation. Increased understanding of how standing genetic variation influences organism response to future changes in thermal conditions is important given that temperature is predicted to be a key driver of future community and population dynamics in phytoplankton around the globe (Anderson et al., 2021; Barton et al., 2016).

Recent model intercomparison studies have pointed to an urgent need to reduce uncertainty in the projected responses of marine ecosystems to climate change to help support human adaptation planning (e.g., Tittensor et al., 2021). Here, in line with this overarching research objective, we examined temperature–growth relationships both among and within species of cold-adapted diatoms, a group of taxonomically diverse SO phytoplankton (Hasle, 1969) that can generate >65% of primary production in the SO (Uitz et al., 2009) and are responsible for a disproportionately large fraction of global organic carbon export to the deep sea (Buesseler, 1998; Smetacek et al., 2012). We tested the hypothesis that adaptively relevant intraspecific variation in thermal functional traits is characteristic of SO diatom communities, and that such trait variation can meaningfully alter trait-guided predictions of future diatom biogeography in a warming SO. We investigated the thermal growth performance of 43 recently collected SO diatom strains, representing seven phylogenetically diverse species, across a wide range of ecologically relevant temperatures. For a majority of strains, we estimated three ecologically important thermal performance traits: optimal temperature for growth (T_{opt}), maximum temperature for growth (T_{max}), and maximum acclimated growth rate (μ_{max}). We then used projections of future SSTs in tandem with our newly estimated thermal traits to illustrate the sensitivity of future species-level diatom biogeography to strain-level trait variance. The observed patterns in thermal trait variation suggest that SO diatoms will persist in the face of expected SST change. Our study highlights the important role that strain level variation could play in future biogeographic outcomes of climate-change driven alterations in the marine environment.

2 | METHODS

2.1 | Experimental strains

Thermal phenotyping was conducted on 43 strains representing seven cold-adapted species, all collected aboard the R/V *Nathaniel B. Palmer* NBP-1701 from surface waters at 15 localities near to or south of the Polar Front in the Pacific sector of the Southern Ocean between 29 December 2016 and 16 January 2017 (Figure 1; Table S2). Individual cells or colonies were isolated by a dissection microscope (Olympus SZX16) from whole seawater, rinsed three times with sterile 0.2 μm filtered seawater and placed into f/20 media (Guillard & Ryther, 1962) at 2–4°C, and grown under continuous light (80–100 μmol photons m^{-2} s^{-1}) to simulate summertime light conditions in the SO. Isolates were then maintained in batch culture at 2°C under 24 h continuous low light (40 μmol photons m^{-2} s^{-1}) to limit growth rates and were transferred monthly into fresh f/2 media for approximately 20 months until used in the experiments described below.

2.2 | Strain identification

Isolated strains were identified to species using the 18S rDNA sequence. Cellular biomass from 200 to 1000 μl aliquots of late-stationary culture was collected via vacuum filtration onto 96-well 0.2 μm MultiScreen® plates (Merck) and stored at −80°C until extraction. Genomic DNA was extracted using the DNeasy 96 Plant Kit (Qiagen) following the manufacturer's protocol, with an adjustment to the initial lysis (65°C for 10–20 min) to increase yield. The 18S

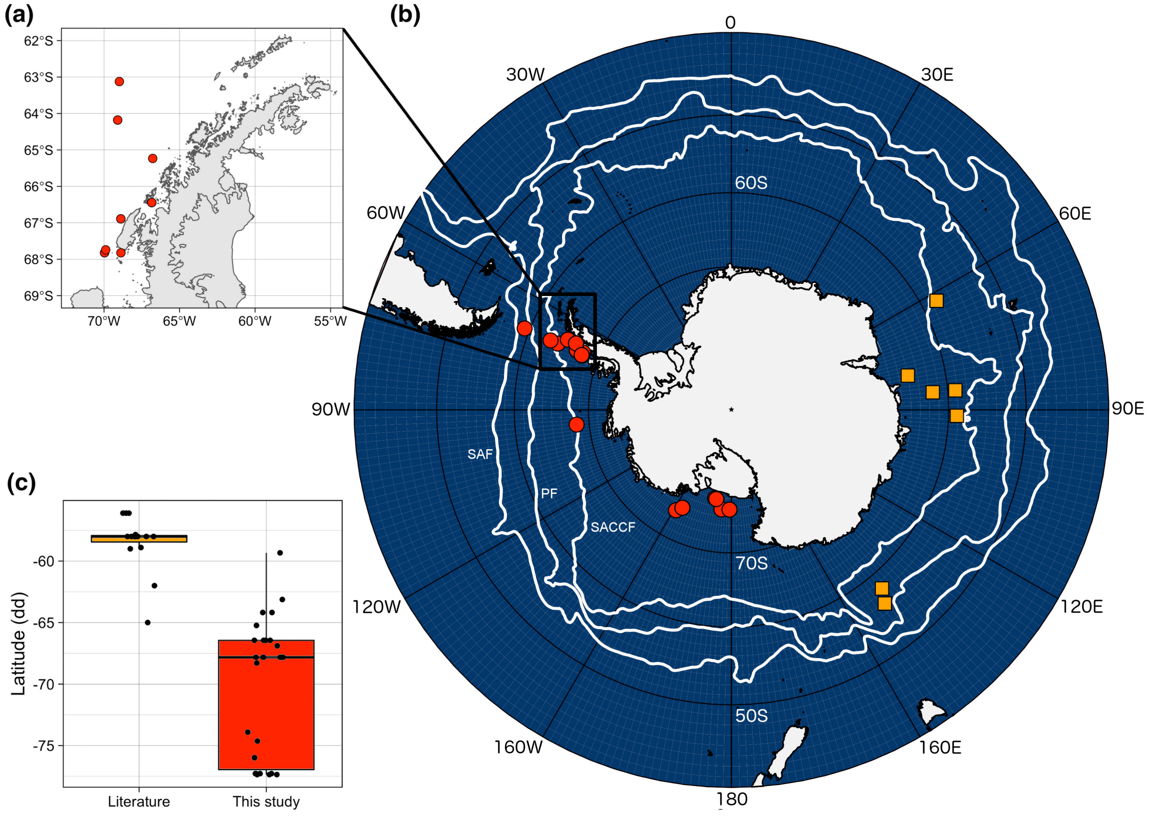

FIGURE 1 Overview of sample sites. (a) West Antarctic peninsula (WAP) sample sites. (b) Fifteen sample sites for 43 diatom strains examined in this study (red circles) and seven sites from 12 previously published thermal performance curves (orange squares; Table S1). White lines represent mean meridional placement, from north to south, of the Subantarctic Front (SAF), Polar Front (PF) and Southern Antarctic Circumpolar Current Front (SACCF) (Park et al., 2019) and the asterisk indicates the South Pole. (c) A comparative boxplot showing the more poleward latitudinal origin of strains characterised in this study versus those found in the literature. [Color figure can be viewed at wileyonlinelibrary.com]

rDNA was amplified using a 15 μl reaction mixture containing ~0.5 ng DNA, 1X colourless GoTaq master mix (Promega), and 0.5 μmol L^{-1} each of the universal 18SA and 18SB primers (Medlin et al., 1988) in a thermocycler (Eppendorf AG 22331 Mastercycler) at 94°C for 2 min, 40 cycles of 94°C for 30 s, 60°C for 60 s, and 72°C for 2 min followed by 10 min at 72°C. PCR amplicons were then purified by ethanol precipitation (e.g., Zeugin & Hartley, 1985) and quantified by Nanodrop (ThermoFisher Scientific). Amplicons were sequenced unidirectionally using the reverse primers only either on a 3500XL Genetic Analyzer (Applied Biosystems) at the University of Rhode Island Genomics and Sequencing Center, or on an ABI 3730XL (Applied Biosystems) at Yale University's Keck DNA Sequencing Facility. Sequences were analysed using Genomics Workbench software, V9.0.1 (Qiagen) and BLAST (Altschul et al., 1990). The resulting partial 18S rDNA sequences for strains examined in this study were submitted to NCBI (accession numbers ON678208–ON678250). Twelve of these strains were submitted to the National Center for Marine Algae and Microbiota (NCMA; Table S2).

Although partial 18S sequencing cannot confirm that the above strains represent unique genotypes, marine diatom population genetic studies have shown extremely high clonal diversity among individuals and minimal re-sampling of clones, even for individual diatoms isolated from the same water samples (Godhe & Rynearson, 2017). This recurring pattern in the literature in conjunction with the broad spatial sampling for this study supports our operating assumption that these strains represent a reasonable spread of intraspecific genetic diversity.

2.3 | Literature reports of Southern Ocean diatom thermal performance

Fifteen comparable thermal performance curves (TPCs) for SO diatom strains were identified in the literature (Figure 1; Table S1). These strains had growth rate data for more than three temperature levels and reasonably similar light (~70–150 μmol photons m^{-2} s^{-1}) and nutrient (saturating) conditions to the strains examined in this study. They are presented herein to emphasise the relative paucity of diatom thermal trait variation for the SO at both the specific and strain levels, especially at higher latitudes.

2.4 | Experimental conditions and data collection

We designed and used a thermal gradient plate to conduct multi-environmental growth assessments (hereafter the MEGAplate) of 43 strains across a temperature gradient. The MEGAplate is a large rectangular tabletop aluminum slab with a 1″ diameter hole drilled across each end, from back to front (Figure S4). A pump circulates chilled coolant through the bore holes at either end of the MEGAplate, and when coolant is chilled at two discrete temperatures, a continuous temperature gradient is formed across the plate. The aluminum plate and hosing are foam-insulated except where microtiter plates are located on the plate. To ensure full contact and temperature transfer between the thermal block and the experimental microtiter plates, small aluminum plates were custom-machined to snugly fit into the base of standard 48-well microtiter plates.

Five identical randomised 48-well microtiter plates were inoculated with experimental strains taken from our lab-maintained culture libraries and placed at five locations along the MEGAplate thermal gradient (0, 1.5, 3.0, 4.5, and 6°C). Strains were grown in 1 ml of f/2 media (33 psu) under uniform 24 h continuous lighting (130 µmol photons m^{-2} s^{-1}, continuous cool white LED light), which is representative of regional in situ conditions during the austral summer (Australian Antarctic Program, Australian Department of Agriculture, Water and the Environment, n.d.). Following a standard protocol (Boyd et al., 2013; Brand et al., 1981), replicate measurements were conducted in sequence, by measuring the same treatment over many sequential growth cycles. This maximised strain number on each 48-well plate at each temperature. Pilot work and intermittent measurements across each microtiter plate on the MEGAplate indicated that temperatures in each well varied by ±0.1°C. Because many of the chosen strains unexpectedly grew at temperatures >6°C, additional temperature treatments of 7.5, 10.0, and 12.5°C were grown in microtiter plates in upright incubators (Percival) under identical experimental conditions. Sub-zero temperatures were not assayed because our focus was on the thermal optima and maxima allowing us to avoid experimental complications associated with freezing seawater and variable salinities.

2.5 | Temperature acclimation and fluorescence measurement

Prior to conducting growth rate measurements, all 43 strains were acclimated to treatment temperatures in a step-wise fashion. The three lowest temperature conditions (0, 1.5, and 3°C) were seeded directly from the low light batch cultures described above and were allowed to acclimate to the higher light conditions for 7 days before transfer into fresh media and determination of growth. Cells were acclimated incrementally to temperature treatments of 3°C and higher via a series of transfers into fresh media and 1–2°C temperature increases followed by at least 7 days of acclimation. Specific growth rate (μ) was determined by relative change in chlorophyll *a* fluorescence during exponential growth. Bulk fluorescence for all treatments was measured every 1–4 days between inoculations into fresh media (excitation: 455 nm, emission: 680 nm; Molecular Devices M5 Microplate Reader). Treatment plates were kept on ice in the dark for 10+ min before each measurement. Raw fluorescence reads were omitted from μ estimation if a sample was visually determined to be dead or contaminated. Up to 20 replicate cycles of growth were measured for each strain at each temperature.

2.6 | Growth rate determination

For each growth cycle, μ was determined by fitting a log-linear regression for all possible consecutive 3–4 point segments of a fluorescence over time growth curve in a sliding window fashion. The steepest slope was used to determine maximum growth rate (e.g., Samuels et al., 2021) and moved forward for subsequent analysis. Three criteria were applied to restrict the dataset to only the highest quality growth rates. First, growth cycles were excluded if they contained fewer than three fluorescence measurements. Next, growth cycles were excluded if the r^2 value of the regression was <.9. Finally, if the initial growth rate was also the lowest rate measured, we conservatively assessed that strain to still be acclimating, and removed it from the dataset. This resulting high-quality growth rate dataset has been deposited at the U.S. Antarctic Program Data Center (Bishop, 2021).

2.7 | Thermal performance at 1.5°C

High-quality specific growth rates were filtered to all rates collected at 1.5°C, the assay temperature most closely corresponding to mean SSTs for the SO regions sampled (Figure S2), and were analysed for differences among both species and strains. After demonstrating homogeneity of variance among species using Bartlett's test in the R package stats (R Core Team, 2020), among-species differences were tested using a one-way ANOVA followed by Tukey's post hoc analysis. For each species, the scale of among-strain differences in growth rate at 1.5°C was assessed by calculating coefficients of variation.

2.8 | TPC modelling and trait derivation

Thermal performance curves were estimated by fitting a modified Norberg function (Norberg, 2004; Thomas et al., 2012) to quality-filtered growth rates (Table S3; Figure S5). This particular function was chosen because it has been shown to perform well in diatoms compared with more than a dozen alternative models (Low-Décarie et al., 2017). TPCs were estimated only for the strains for which a thermal maximum was encountered during the experiment (26/41 strains). TPCs were fitted using growthTools (Kremer, 2020), which returns expected values and 95% confidence intervals for four Norberg equation parameters (T_{opt}, w, a, and b).

Inter- and intra-specific variation was determined for the following traits; thermal optimum (T_{opt}), maximum temperature for growth (T_{max}), and maximum growth rate (μ_{max}, or specific growth rate at T_{opt}). These traits were determined using a bootstrapping approach, whereby random TPCs were repeatedly sampled with replacement ($n = 1000$) from each strain's best-fit parameter space. Bootstrapped sample distributions for each trait were summarised by their mean and standard error for each strain. For cross-species hypothesis testing, Kruskal–Wallis tests followed by post hoc Conover–Iman tests were conducted because a Bartlett test indicated that variance was not homogeneous among groups for two of the three traits (Table S4). The relative magnitude of intraspecific variability across species was assessed by coefficient of variation using bootstrapped point estimates. We note that the minimum temperature for growth (T_{min}) was not reported as a focal trait because of the overall positive growth rates at 0°C, as well as the greater relevance of temperature change at the middle and upper ends of the growth performance curves with regards to projected increases in SST.

2.9 | Illustrating geographic range variance by species

Future geographic ranges for each species were calculated using the average maximum annual SSTs predicted for the years 2070–2099 for the global ocean south of 40°S (Figure S6). SST raster data were retrieved from a mean of CMIP5 monthly RCP 8.5 scenario runs (1.25° resolution grid from the KNMI Climate Explorer, accessed 2019; van Oldenborgh et al., 2009). Each strain's geographic range is conservatively defined here as the spatial area wherein its estimated T_{max} exceeds average annual maximum temperature. Geographic ranges were calculated for five of seven species because for two species only one TPC was available. Strains with the smallest and largest T_{max} estimates for each species were chosen for analysis.

2.10 | Data munging, visualisation, and statistical analysis

All data munging, visualisation, and statistical analyses were conducted in R (R Core Team, 2020). Maps were constructed in R using the sp (Pebesma & Bivand, 2005), sf (Pebesma, 2018), raster (Hijmans, 2020), and stars (Pebesma, 2021) packages. Coastline shapefiles were accessed from the British Antarctic Survey Geodata Portal (Gerrish et al., 2021), and estimates of polar front locations from recent work by Park et al. (2019).

3 | RESULTS

The 43 strains examined here were collected along a 5000 km transect across the Pacific sector of the Southern Ocean (Figure 1) and identified to species using partial sequences of the 18S rRNA gene. Alignments to top blastn hits for each sequence query had >99% similarity to existing entries in the NCBI nt database. Seven species representing six genera were identified (Table S2). Partial 18S sequences for each strain are available at NCBI (accession numbers ON678208–ON678250) and 12 representative strains were deposited at the NCMA (Table S2).

Of the 2821 acclimated specific growth rates determined at temperatures ranging from 0 to 12.5°C, 2014 passed our quality control threshold (Figure S1; Table S2). At 1.5°C, an intermediate SST commonly experienced in the native habitats of the SO diatom isolates (−59 to −77°S) during the austral summer (Figure S2), mean specific growth rates among individual isolates varied by threefold (0.12–0.35 day^{-1}; Figure 2a) and were significantly different among species (Figure 2a; Table S5; $F = 9.501$, df = 6; $p < .001$, Tukey's adjusted $p < .05$). Within species at 1.5°C, growth rate coefficients of variation for all seven species ranged from 10% to 23% (Figure 2b; Figure S3).

We then measured growth rates from 0 to 12.5°C and modelled TPCs for 26 strains to assess species- and strain-level growth responses to thermal conditions (Figure 3; Table S3). Significant among-species variation was observed for all three traits (Table S4), with mean T_{opt}, T_{max} and μ_{max} values per species ranging from 2.0 to 4.6°C ($\bar{x}$ = 3.64°C), 4.9–10.4°C ($\bar{x}$ = 5.40°C) and 0.23–0.37 day^{-1} ($\bar{x}$=0.30 day^{-1}), respectively (Figure 3; Table S5). The TPC models of five strains were poorly fitted to the data (Table S3). In some instances, the poor fit of a single strain (*Thalassiosira tumida* #2563) did not strongly alter the broader thermal performance patterns of the species (i.e., there were several good *T. tumida* strain models) or poor fits were associated with a species represented by just a single strain (*Pseudo-nitzschia subcurvata* #2317).

Thermal traits also varied within species (Figure 4; Table S6) and the magnitude of variation was both trait- and species-specific. For example, T_{opt} varied by up to 5.5°C among strains within a single species whereas T_{max} varied by up to 7.5°C. However, not all species had equal magnitudes of variation in their thermal traits. *Actinocyclus curvatulus* strains, for example, were found to vary strongly in all three traits, with T_{opt}, T_{max} and μ_{max} differences as much as 5.5°C, 7.5°C and 0.15 day^{-1}, respectively. By contrast, *Stellarima microtrias* traits varied by much less (1.8°C, 1.6°C, and 0.08 day^{-1}, respectively). The species-specific trait variation in these examples is further reflected in high coefficients of variation, in particular for T_{opt} (26%–48%) but also in T_{max} (up to 36%) for multiple species.

4 | DISCUSSION

The adaptive potential of phytoplankton will likely play an important role in their short- and long-term responses to climate change (Collins et al., 2014; Martiny et al., 2022; Rynearson et al., 2022). Given the ecological and biogeochemical importance of phytoplankton and increases in SST taking place in the SO (Fan et al., 2014; Tonelli et al., 2021), the capacity of phytoplankton to adapt to and grow in elevated SST has immediate relevance. We assessed one aspect of phytoplankton adaptive potential, standing trait variation, by measuring more than 2000 high quality growth rates across 43 strains representing seven diverse diatom species. This work represents a substantially broader inclusion of intraspecific

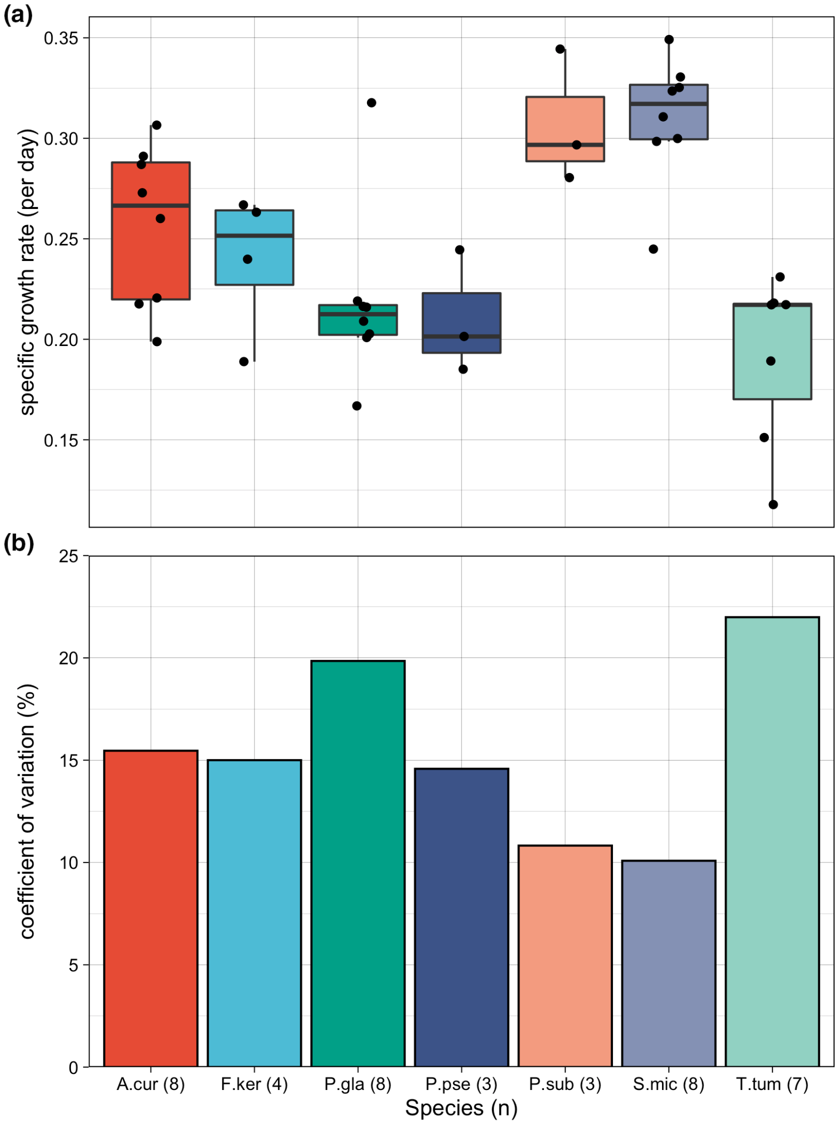

FIGURE 2 Specific growth rate variation among species at 1.5°C. (a) Boxplot comparing specific growth rates for each of 41 strains across 7 species. See Figure S3 for growth rates of individual strain. Two strains not included (2190 and 2412) as they have only a single data point at 1.5°C. (b) Bar plot comparing coefficients of variation in growth rate among species. Strain number per species indicated in parentheses at the *x*-axis. Species abbreviations: *Actinocyclus curvatulus* – A.cur; *Fragilariopsis kerguelensis* – F.ker; *Porosira glacialis* – P.gla; *Porosira pseudodenticulata* – P.pse; *Pseudo-nitzschia subcurvata* – P.sub; *Stellarima microtrias* – S.mic; *Thalassiosira tumida* – T.tum. [Color figure can be viewed at wileyonlinelibrary.com]

variation than previous efforts for phytoplankton taxa both globally (Anderson et al., 2021; Thomas et al., 2012) and from polar habitats (Boyd, 2019; Boyd et al., 2013). We found evidence of significant growth performance variance both within and between phytoplankton species, lending support to our hypothesis that meaningful thermal trait variance is characteristic of SO phytoplankton communities and that this standing trait variation may underlie important evolutionary potential in polar marine ecosystems.

Thermal trait variation was observed at 1.5°C, a commonly experienced SST in the SO during austral summer, revealing low and highly variable specific growth rates (0.12–0.35 day^{-1}). These rates translate to generation times ranging from roughly 2–6 days and correspond well to mean growth rates of other polar taxa at similarly low temperatures (Boyd et al., 2013; Thomas et al., 2012). Both the magnitude of the rates as well as their variability also align well with growth rates at near zero temperatures of temperate phytoplankton, for example various *Skeletonema* taxa in the northwest Atlantic (Anderson & Rynearson, 2020), suggesting that growth rate variability at low temperatures may occur broadly across marine phytoplankton taxa.

4.1 | Trait variance among and within phytoplankton species

Thermal growth traits are important measures of biological preference and tolerance, which unlike point estimates of growth performance, can be applied in broader efforts to parameterise global biogeochemical models (Longhurst, 1998) and assess present and future biogeography (e.g., Anderson et al., 2021), among other uses. The 26 new TPCs and their derived thermal traits reported in this study greatly expand the number of TPCs available for SO phytoplankton, especially with regard to strains and taxa that inhabit very high latitudes (Figure 1), where projected future increases in SST are significant (Moore et al., 2018). Strain-level variance in T_{opt} was up to 2–3× greater in our SO diatoms than in temperate diatom species (Anderson & Rynearson, 2020; Boyd et al., 2013), suggesting that SO diatom species have broad thermal optima that are unlikely to be captured by the analysis of a single strain. T_{opt} was higher than SSTs at the time of strain isolation (Table S2) and SSTs south of the polar front during austral summer (Figure S2), a pattern often observed in

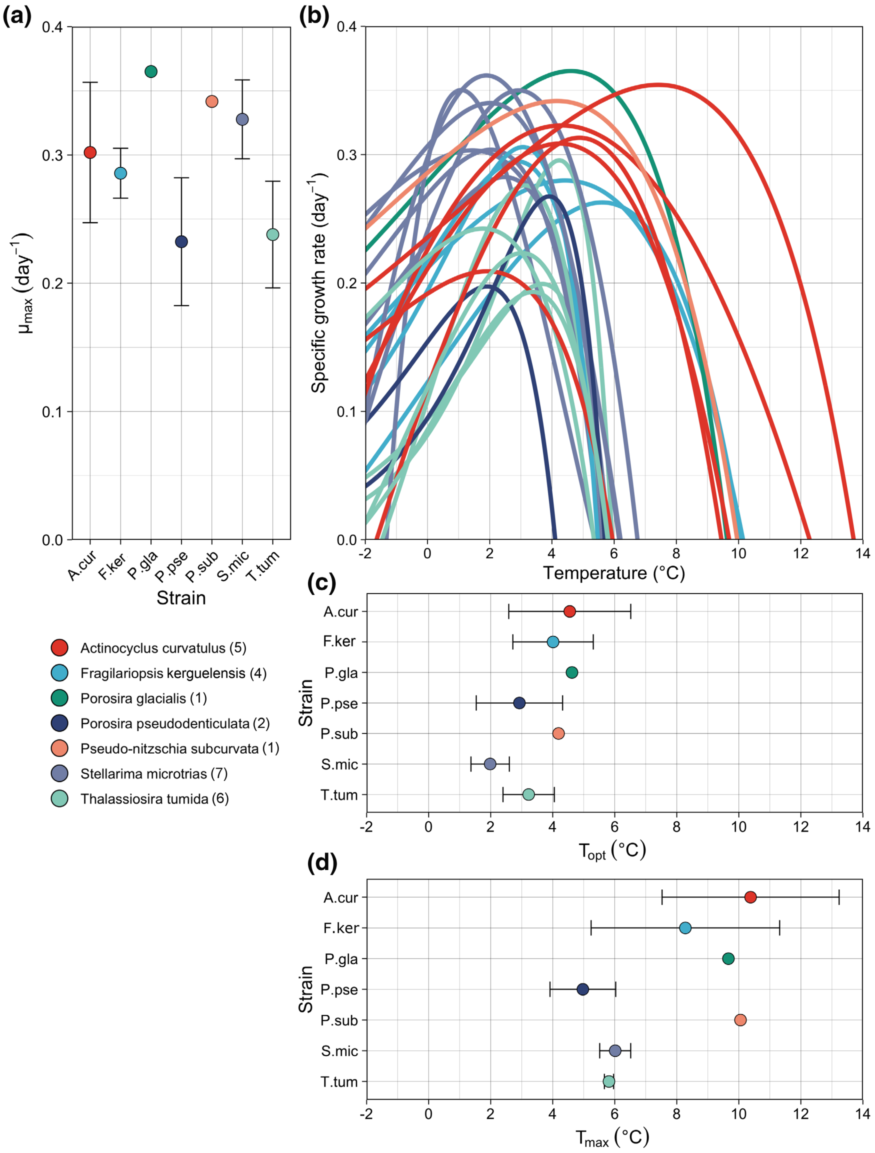

FIGURE 3 Modelled thermal performance curves for 26 strains. (b) Panel showing all 26 TPCs; colour indicates species. (a, c, d) scatter plots along axes illustrate species-level mean and standard error for the following three thermal traits: Maximum specific growth rate (μ_{max}; a), temperature for optimal growth (T_{opt}; c) and thermal maximum growth (T_{max}; d). See Figure S5 for strain-specific TPCs. Lower bounds of each thermal niche (e.g., thermal minima) were not determined to avoid experimental complications associated with freezing seawater and variable salinities. [Color figure can be viewed at wileyonlinelibrary.com]

diverse taxonomic groups (e.g., Deutsch et al., 2008), including phytoplankton (Anderson et al., 2021). This difference between physiological potential and experienced thermal environment is referred to as the thermal safety margin (e.g., Anderson et al., 2021) and may be indicative of a broader and possibly adaptive persistence to warming for phytoplankton at high latitudes.

The thermal limits of growth (T_{max}) for individual species will ultimately dictate the geographic extent of polar species in the face of increased SSTs. Here, we found that strain-level variation in T_{max} differed significantly among species, which may help to explain historical differences in occurrence among them. For example, the relatively large variation in T_{max} of *Fragilariopsis kerguelensis* may be related to its numerical dominance and broad geographic distribution across the SO and subantarctic waters (Pinkernell & Beszteri, 2014). By contrast, T_{max} in *T. tumida* and *S. microtrias* were significantly less variable among strains. These species are associated with sea ice and their historical occurrence is tightly linked to sea-ice presence and the seasonal marginal sea ice zone (Armand et al., 2005; Hasle, 1969; Zielinski & Gersonde, 1997). This apparent limitation to habitat south of the maximum sea ice extent, where phytoplankton are estimated to experience relatively narrow thermal ranges (Doblin & van Sebille, 2016), may explain the lack of variation in T_{max} in these sea ice-associated species.

4.2 | Thermal tolerance variation and biogeographic range estimation

Future changes in SST may influence the biogeography of polar phytoplankton, resulting in viable range shifts (Anderson et al., 2021) and leading to downstream changes in food web dynamics and the biogeochemical cycles to which they are tied, such as changes in primary production (Dutkiewicz et al., 2013) and elemental export to both the deep sea (Assmy et al., 2013) and lower latitudes (Sarmiento et al., 2004). These shifting biogeographies, including their evolving range limits, are tied to thermal tolerance-associated functional

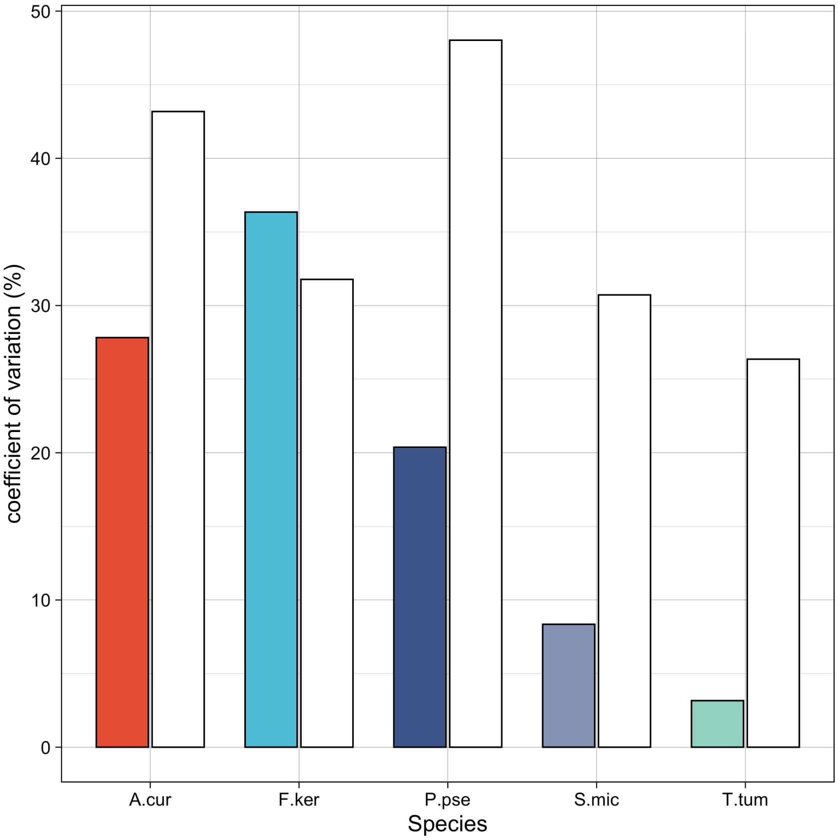

FIGURE 4 Coefficients of variation (CV) among species for T_{max} (filled) and T_{opt} (unfilled). Species with only one tested strain (*Porosira glacialis* and *Pseudo-nitzschia subcurvata*) were omitted. [Color figure can be viewed at wileyonlinelibrary.com]

traits, such as T_{max} (Comte & Olden, 2017; Kellermann et al., 2012). For this set of SO diatoms, T_{max} ranged from 4.1 to 13.7°C between species and by up to 7°C among strains within species, which led us to examine how strain-level differences might affect SST-based predictions of future species ranges in the SO. We estimated potential geographic ranges for the most and least thermally tolerant strains for each species by mapping their T_{max} values onto average maximum annual SSTs projected for the years 2070–2099 (CMIP5 RCP8.5; Figure S6). Under this extreme warming scenario, the areal extent of viable habitat differed by up to 97% between the least and most thermally tolerant strains for each species (Figure 5). For all five species, we found that the T_{max} values for the least thermally tolerant strains resulted in a geographic extent restricted to waters south of the Polar Front. By contrast, the predicted ranges of the most thermally tolerant strains varied greatly in their northward reach, with some approaching the subtropical front (STF), in effect encompassing the entire Southern Ocean. While such predictions are coarse and do not include the likely rapid evolution of these trait values (a factor not often incorporated into such estimates), they broadly illustrate the importance of species-specific trait variability.

Our predictions of biogeographic ranges correspond reasonably well with previous projected ranges and historical occurrence data. For example, recent species distribution modelling estimated that the range of *F. kerguelensis* might extend up to and beyond the STF, both now and in the future (Pinkernell & Beszteri, 2014), which is in good agreement with our estimated maximum range extent (Figure 5). The combined findings of both occurrence- and trait-based range projections suggest that this species, which contributes significantly to carbon export in the SO (Zielinski & Gersonde, 1997), may be robust to expected regional SST change. While there are no prior species distribution estimates for the other species examined in this study, their ranges also largely agree with historical occurrence, and are thus projected to be tolerant of future SST conditions south of the Polar Front. The single exception to this correspondence with historical occurrence data is for *A. curvatulus*, which we predicted to have a more expansive geographic range than observations for either it (not frequently documented) or the more frequently observed congeneric *Actinocyclus actinochilus* might suggest. Notably, this latter taxon has a bi-polar distribution (Zielinski & Gersonde, 1997), and a wide thermal niche which may promote dispersal and gene flow between very geographically distant populations. Altogether, our projections suggest SO phytoplankton might already harbour the phenotypic diversity required to withstand projected 21st century SST change in the SO.

Our geographic range projections illustrate that the common focus on species-level trait variation, at the expense of considering strain-level variation, is likely insufficient to accurately describe species-level attributes and interactions, such as future thermal niche differences and putative competition between SO endemics and encroaching temperate taxa. Although our strains were collected across a 5000 km transect, it is expected that more strain level variation exists across the much larger SO. Our findings also have implications for Arctic phytoplankton species and communities, which have shown similar strain-level trait diversity (Wolf et al., 2019) and are subject to even greater levels of SST rise

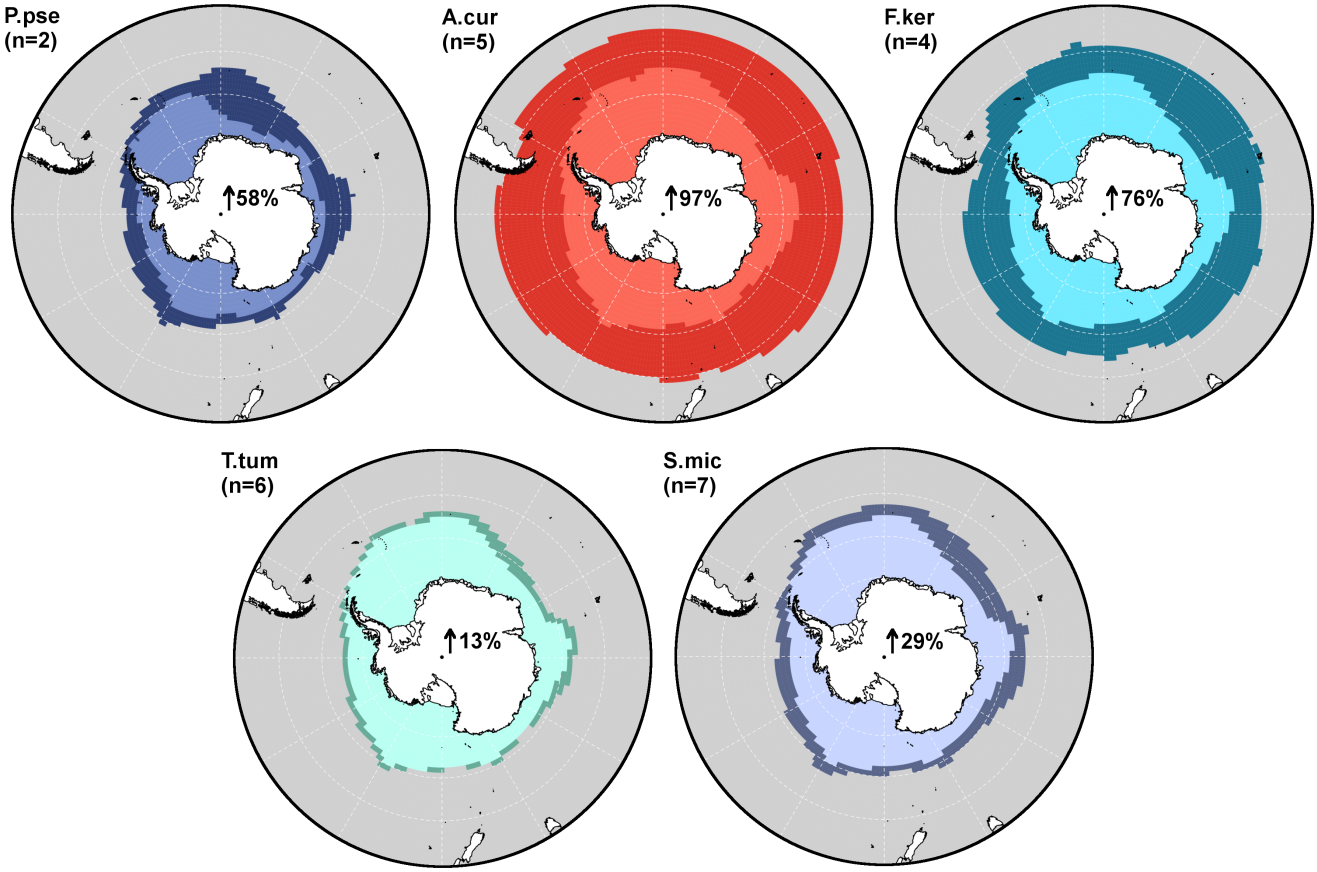

FIGURE 5 Maps illustrating that the predicted future geographic ranges of five SO phytoplankton are highly dependent on intraspecific variation in T_{max}. Lighter shades indicate core range, where all strains tested are theoretically able to grow (range is therefore defined by the least tolerant strain of each species). Darker shades represent the geographic range of each species as defined by its most thermally tolerant strain, where at least one strain out of those tested could theoretically grow. Potential ranges are predicted by model projections of mean maximum annual temperature for the period 2070–2099 and each strain's thermal maximum. Species with one tested strain (*Porosira glacialis* and *Pseudo-nitzschia subcurvata*) are not included. Percent differences between core and extreme species ranges are indicated on each globe. Dot to left of arrow indicates south pole. [Color figure can be viewed at wileyonlinelibrary.com]

(Meredith et al., 2019). Our work revealed that phenotyping even a handful of individual strains can reveal potential range differences that span hundreds of thousands of square kilometers, providing a more holistic view of species-specific thermal preference and more refined predictions of future thermal habitat.

4.3 | Potential eco-evolutionary outcomes of phytoplankton thermal trait variation

While our results suggest a prominent role for adaptive lineage sorting rooted in thermal trait variance, recent findings make it clear that thermal trait adaptation via de novo variation could also play an adaptive role in phytoplankton, including diatoms. For example, the diatom *Thalassiosira pseudonana* evolved elevated T_{opt} values through de novo mutation within 300 generations in both uniform and fluctuating thermal environments (Schaum et al., 2018). Similar findings of rapid mutation-based evolution of thermal traits exist for the model coccolithophore *Emiliania huxleyi* (Listmann et al., 2016; Schlüter et al., 2014). At the specific growth rates we measured here, 300 generations correspond to approximately 10–30 years of austral summer growth (just 2 months per year; Soppa et al., 2016), providing initial timelines of evolutionary change in the absence of genotypic variation. Increased incorporation of genotypic diversity into evolution experiments is needed to further clarify the relative importance of these two sources of thermal adaptation (Rynearson et al., 2022).

Anthropogenic climate change poses a significant risk to the historical composition of communities in diverse ecosystems worldwide (Buisson et al., 2013; Fourcade et al., 2019; Gaget et al., 2021), including for SO phytoplankton (Schofield et al., 2017). One important consequence of large intraspecific differences in thermal tolerance among SO phytoplankton is that this trait variability may interact with other plastic phenotypes to shift species composition and alter broader ecosystem processes. The shape and size of this effect will depend on the degree to which thermal traits covary among individuals/populations, with greater trait covariance leading to stronger effects and vice versa. The implications of this relationship were recently illustrated at the phytoplankton functional group level by Barton and Yvon-Durocher (2019), whose trait observations suggested that a transition from lower to higher T_{opt} communities could result in a simultaneous transition in other co-varying traits, including cellular C, N, and chlorophyll *a* content. Similar relationships may exist in polar and intraspecific contexts as well. For example, the Antarctic diatom *P. subcurvata* examined here is known to produce domoic acid, a neurotoxin that affects the vertebrate nervous system, and this capacity varies by genotype (Olesen et al., 2021). We found moderate levels of genotypic variation in growth rate among *P. subcurvata* strains and if co-variance among phenotypes exists, it could potentially drive a shift in toxin production as SO SSTs rise, affecting seabirds and mammals that are key components of the SO ecosystem (Bestley et al., 2020). It should also be noted that such hypotheses are complicated by the fact that it is still unclear which traits covary with T_{opt} (but see O'Donnell et al., 2018), or which other environmental drivers may affect its capacity to rapidly evolve—more multi-driver experiments on phytoplankton are needed to address this knowledge gap further (Boyd et al., 2018). For example, there is experimental evidence that low nutrient levels limit adaptation to warming in temperate diatoms (O'Donnell et al., 2018), and that T_{opt} is a saturating function of nitrate concentrations (Thomas et al., 2017), suggesting that even though temperature tolerance has the capacity to evolve rapidly under otherwise ideal conditions, interactions with changes in nutrient levels in particular may limit this capacity being fully realised. Overall, much of the importance attributed to relevant fitness-proxy variation (e.g., growth rate differences at predicted SSTs) is reliant on correlated trait variation in other ecologically and biogeochemically important phenotypes, underscoring the need to assess both in future studies concerning ecosystem sensitivity to rapidly changing thermal environments.

4.4 | MHWs and thermal performance variation

The predicted ecological implications of thermal trait variation in SO phytoplankton are not limited to long-term effects. Acute events such as marine heatwaves (MHWs), which have increased both in magnitude and duration over the past 50 years and are predicted to intensify over the coming century (Frölicher et al., 2018), may interact with standing thermal trait variation to induce different stress responses within and among phytoplankton populations. For example, Samuels et al. (2021) recently subjected thermally diverse strains (e.g., those with distinct TPCs) of the endemic SO diatom *A. actinochilus* to simulated heatwaves and identified genotype as the factor of greatest effect size in explaining variation in pre- and post-heatwave growth rates, ahead of both acclimation temperature and cumulative heatwave intensity. Our determination of widespread intra- and inter-specific thermal trait variation in the SO suggests that summertime MHWs in the Ross Sea or along the West Antarctic peninsula could act over short time scales to restructure blooming phytoplankton communities at multiple taxonomic levels, potentially accelerating lineage selection and hastening local adaptation in a species-specific manner. In this context, rapid directional selection could be beneficial in the long run, with mean trait values moving towards optima more in line with future SO SSTs. Ultimately, the relative impact of such acute lineage selection on the evolutionary potential of SO phytoplankton will depend on more than standing genetic and phenotypic variability, including other important population genetic parameters (which are also poorly constrained in diatoms as a group), such as base mutation rates (Krasovec et al., 2019), recombination rates, and the degree of genetic connectivity among blooming regions (Whittaker & Rynearson, 2017).

Overall, our results indicate that within-species variation in thermal tolerance is significant and may play an important role in shaping the future abundance, community composition and location of polar phytoplankton. Our work here supports a recognised and urgent need to reduce uncertainty in how marine ecosystems will respond to climate change (e.g., Tittensor et al., 2021) by revealing the scale of thermal physiological variation in diatoms, a key phytoplankton taxon at the base of SO food webs. Importantly, our findings suggest these communities may already harbour the thermal trait diversity required to withstand projected 21st century SST change in the SO even under severe climate forcing scenarios.

AUTHOR CONTRIBUTIONS

Ian W. Bishop, Tatiana A. Rynearson and Sinead Collins conceived of and designed the study; Stephanie I. Anderson, Tatiana A. Rynearson and Sinead Collins isolated diatom strains from the field; Stephanie I. Anderson and Tatiana A. Rynearson designed and built the MEGAplate; Ian W. Bishop collected and analysed growth data and all authors contributed to the interpretation of the results and the writing of the manuscript.

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CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Specific growth rate measurements are available through the U.S. Antarctic Program Data Center (USAP-DC) at: https://www.usap-dc.org/view/dataset/601586.

ORCID

Ian W. Bishop https://orcid.org/0000-0003-2197-3197
Stephanie I. Anderson https://orcid.org/0000-0002-2458-0922

Sinead Collins https://orcid.org/0000-0003-3856-4285
Tatiana A. Rynearson https://orcid.org/0000-0003-2951-0066

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SUPPORTING INFORMATION

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